The Atypical Sperm Morphologies of *Aristeus antennatus* and *Aristaeomorpha foliacea* (Crustacea, Dendrobranchiata, Aristeidae) and Their Phylogenetic Significance

Antonio MEDINA

Departamento de Biología Animal, Biología Vegetal y Ecología,
Facultad de Ciencias del Mar, Universidad de Cádiz, Aptdo. 40, E-11510 Puerto Real, Cádiz, Spain

ABSTRACT

The spermatozoa of *Aristeus antennatus* and *Aristaeomorpha foliacea* show two distinct morphological patterns which greatly differ from each other and are also distant from the common dendrobranchiate sperm plan. In *A. antennatus*, the spermatozoon possesses a conspicuous spherical acrosome which lacks both spike and subacrosomal region. Its multilayered inner structure is not comparable to the acrosomal arrangement of any other decapod, and is postulated to be the result of independent evolution. The cytoplasm is concentrated in a collar between the acrosome and the non-membrane bound nuclear material; therefore, it displays a subacrosomal (apomorphic) rather than perinuclear distribution. In spite of the plesiomorphic lack of radial arms, which is common to all dendrobranchiates, the general morphology of this spermatozoon resembles that of reptant decapods in several respects. The absence of a spike, the spherical (not capping) acrosome, and the subacrosomal (instead of perinuclear) cytoplasm are considered as apomorphies. The most significant feature of *Aristaeomorpha foliacea* spermatozoon is the absence of the acrosome. This simple sperm cell consists of the central nuclear material encompassed by a cytoplasmic band that is in turn bounded by the plasma membrane. Typical dendrobranchiate (plesiomorphic) features of *A. foliacea* sperm are the perinuclear cytoplasm (containing small peripheral vesicles, mitochondria and membrane lamellae), the non-membrane bound nuclear material, and the absences of centrioles and radial arms. The two spermatozoal patterns described hereafter appear to be the result of distinct evolutionary trends.

RÉSUMÉ

Les morphologies atypiques des spermatozoïdes d'*Aristeus antennatus* et *Aristaeomorpha foliacea* (Crustacea, Dendrobranchiata, Aristeidae) et leur signification phylogénétique.

Les spermatozoïdes de *Aristeus antennatus* et *Aristaeomorpha foliacea* possèdent des morphologies bien distinctes entre elles et différentes de la morphologie habituelle des Dendrobranchiata. Le spermatozoïde d'*A. antennatus* possède un important acrosome sphérique dépourvu d'épine et de région subacrosomienne. Sa structure interne à plusieurs couches n'est comparable à l'acrosome d'aucun autre Décapode, et on fait l'hypothèse qu'elle est le résultat d'une évolution indépendante. Le cytoplasme est concentré en un collier entre l'acrosome et le matériel nucléaire non limité par une membrane. De ce fait, il montre une distribution subacrosomienne (apomorphe) plutôt que périnucléaire. En dépit de l'absence, plésiomorphe, de bras radiaux, qui est commune à tous les Dendrobranchiata, la morphologie générale de ce spermatozoïde ressemble à celle des Décapodes Reptantia pour plusieurs aspects. L'absence d'épines, l'acrosome sphérique (pas en capuchon), et le cytoplasme subacrosomien (au lieu de périnucléaire) sont considérés comme des apomorphies. La

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caractéristique la plus significative du spermatozoïde d'*Aristaeomorpha foliacea* est l'absence d'acrosome. Ce spermatozoïde simple consiste en un matériel nucléaire central entouré par une bande cytoplasmique, elle-même limitée par la membrane plasmique. Les caractéristiques (plésiomorphes) de Dendrobranchiata du spermatozoïde d'*A. foliacea* sont un cytoplasme périnucléaire (contenant des petites vésicules périphériques, des mitochondries et des lamelles membranaires), le matériel nucléaire non limité par une membrane, et l'absence de centrioles et de bras radiaux. Les deux morphologies de spermatozoïde décrites ici semblent être le résultat de deux tendances évolutives distinctes.

The spermatozoa of dendrobranchiate shrimp are typically described as aflagellate cells consisting of a rounded main body partially encompassed by a cap with a protruding spike [5, 9, 11]. The most prominent feature in this sperm type is the presence of a single appendage, the so-called spike, which characterizes the "unistellate" condition of "natantian" spermatozoa, distinguishing it from the "multistellate" condition of "reptantian" sperm. However, the spike-less sperm morphologies of *Aristeus antennatus* and *Aristaeomorpha foliacea* provide exceptions to the supposed spermatozoal uniformity in the Dendrobranchiata and recommend a thorough analysis of the sperm ultrastructure of both species of Aristeidae. Though DEMESTRE & FORTUÑO [3] briefly described the spike-less spermatozoon of *A. antennatus* from scanning electron micrographs, an accurate characterization requires further investigation by means of transmission electron microscopy. Phylogenetic implications of both dendrobranchiate sperm morphologies will be considered in the context of the decapod sperm configuration.

MATERIALS AND METHODS

Specimens of *Aristeus antennatus* (Risso, 1816) and *Aristaeomorpha foliacea* (Risso, 1827) were collected off the Gulf of Cádiz in October 1993. Small fragments of vasa deferentia including ampullae were fixed in 2.5% glutaraldehyde in filtered seawater for 4-12 h, postfixed in 1% osmium tetroxide and dehydrated through acetones. For transmission electron microscopy, the samples were then infiltrated and embedded in ERL [22]. Ultrathin sections were viewed in a JEOL EX 1200 electron microscope operated at 80 kV.

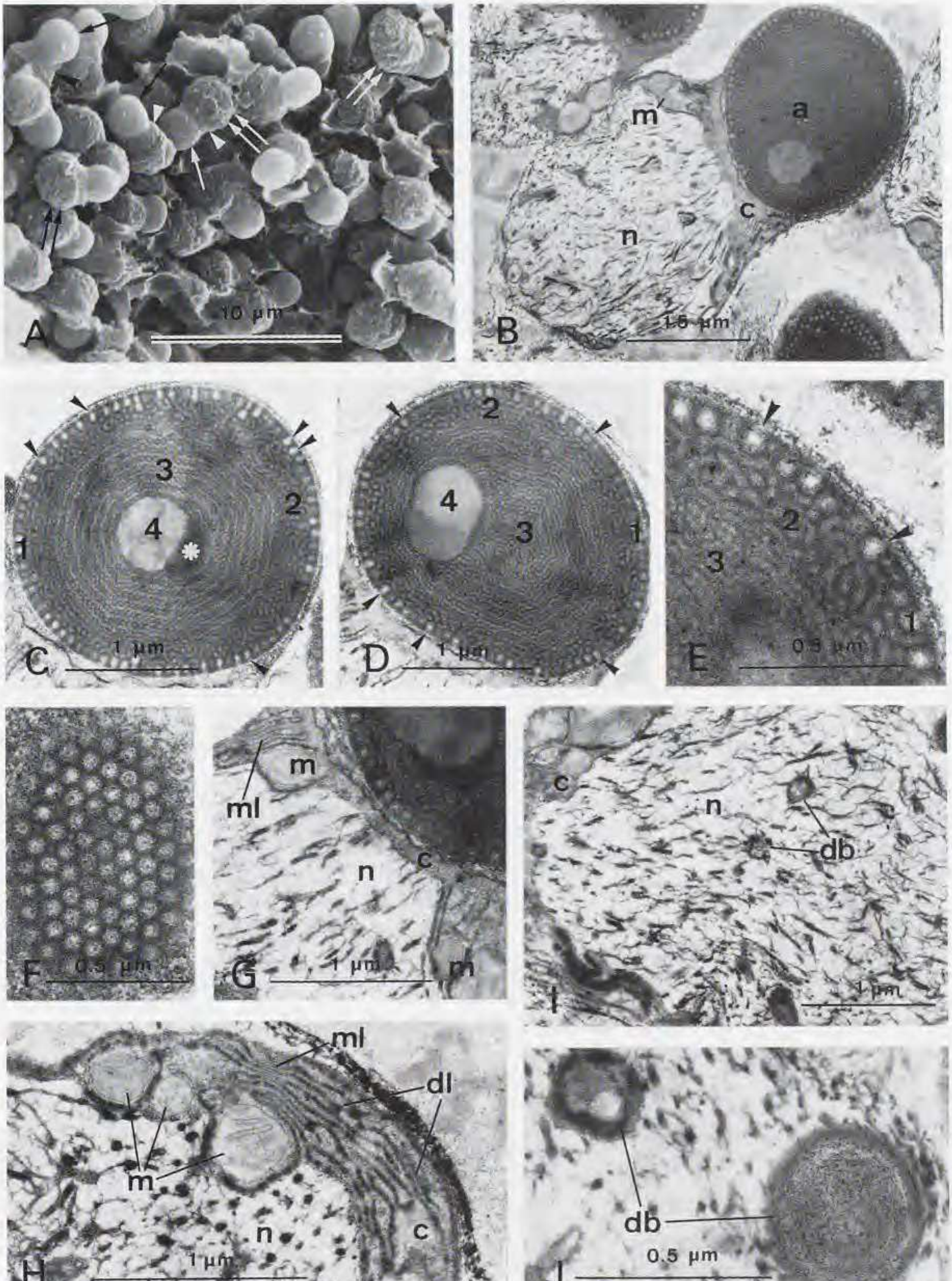
For scanning electron microscopy, following dehydration, the samples were critical-point dried, mounted on copper stubs and sputter-coated with gold. Observations were made on a JEOL JSM 820 electron microscope operating at 20 kV.

RESULTS

Spermatozoon of Aristeus antennatus

The spermatozoon of *Aristeus antennatus* basically comprises a conspicuous and prominent sperical acrosome and the nuclear structure (Figs 1a, b, 3a), the cytoplasmic mass being fairly reduced. The acrosome has a smooth surface, whereas the region containing the nucleus is more irregular in profile (Fig. 1a, b). The whole cell is 5.23 ± 0.33 µm (n = 16) in length. The acrosome measures 2.30 ± 0.16 µm (n = 19) in diameter and the nuclear region 3.02 ± 0.25 µm (n = 16) in width.

FIG. 1. — Scanning (**A**) and transmission (**B-J**) electron micrographs of *Aristeus antennatus* spermatozoa. **A:** Spermatozoa in the ampulla. The acrosome (arrows), cytoplasmic collar (arrowheads) and nuclear region (double arrows) are distinguished. **B:** Sagittal section of spermatozoon. **C-E:** Longitudinal sections of acrosomes showing the complex arrangement of their contents consisting of three distinct layers that correspond to the peripheral layer (1) of small clear vesicles (arrowheads), the marbled-like subperipheral zone (2), and the central region of concentrically arranged material (3). At the innermost region is a clear area (4) that usually appears associated with a dense osmiophilic substance (asterisk). **F:** Tangential section of acrosome through the peripheral vesicle layer. **G, H:** Sagittal (**G**) and oblique (**H**) sections of cytoplasmic collars containing mitochondria and membrane lamellae in continuity with osmiophilic dense lamellae. **I:** The nuclear region of a spermatozoon in sagittal section.. Dense bodies are embedded in the nucleoplasm. **J:** Detail of dense bodies showing myelin-like structure. a, acrosome; c, cytoplasmic collar; db, dense bodies; dl, dense lamellae; m, mitochondria; ml, membrane lamellae; n, nuclear region.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The acrosome is formed by a spherical acrosomal vesicle with structurally complex contents. No distinct subacrosomal region is found. The inner arrangement of the acrosome is symmetrical, since both longitudinal and cross sections show equivalent structural patterns. At the periphery is a single layer of electron-lucent vesicular structures which appear to originate from small invaginations of the acrosome membrane (Fig. 1c-e). Tangential sections show them to be regularly sized (about 80 nm in diameter) and densely packed (Fig. 1f). Immediately under the vesiculate layer, the acrosome materials take on a marbled appearance (Fig.1c, d). The central region of the acrosome is filled with a material arranged in concentric rows of apparently hollow spherical particles (Fig. 1c, d). In many sections, an electron-clear area is observed at the innermost region of the acrosome. It may be centrally located (Fig. 1c) or eccentric (Fig. 1d). A dense material is usually associated with this electron-clear zone (Fig. 1c).

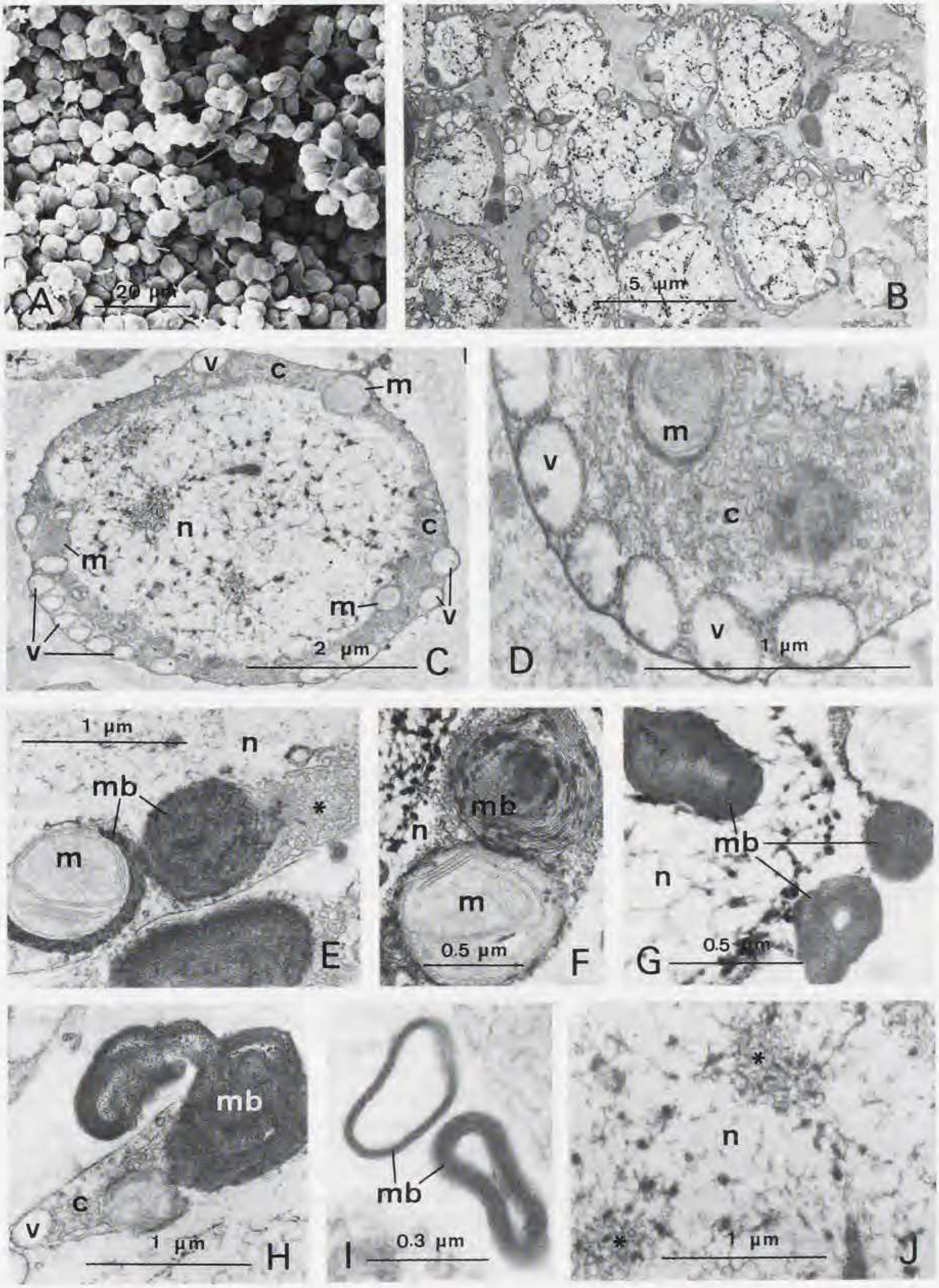
The cytoplasm is reduced to a collar intervening between the acrosome and nucleus which extends laterally over the anterior third of the nuclear region (Figs 1a, b, 3a). The central portion of the cytoplasmic collar shows no noticeable substructure. In contrast, the lateral expansion contains parallel membrane arrays, osmiophilic lamellae and clusters of mitochondria (Fig. 1b, g, h). In favourable sections, osmiophilic lamellae are seen to be in continuity with membrane lamellae (Fig. 1h). Both elements are orientated in the direction of the lateral expansion of the cytoplasmic mass.

The nuclear region contains a non-membrane bound network of chromatin fibres (Figs 1b, h-j, 3a). Anteriorly, the chromatin is surrounded by the cytoplasm, and laterally and posteriorly solely by the plasma membrane. Many fibres appear inserted in the cytoplasmic mass, becoming orientated longitudinally (Fig. 1b, g). Dense bodies and occasional vesicles are observed in the nucleoplasm (Fig. 1i, j). The dense bodies are of membrane origin, since they sometimes show a myelin-like structure (Fig. 1j).

Spermatozoon of Aristaeomorpha foliacea

The sperm of *Aristaeomorpha foliacea* are roundish or slightly ellipsoid cells measuring 5.66 ± 0.79 µm (n = 33) at their widest point. Puzzingly, this dendrobranchiate sperm type does not exhibit any recognizable acrosomal structure (Figs 2a, b, 3b). Thus, the spermatozoon simply consists of the nuclear region and cytoplasm (Fig. 2c). The cytoplasm forms a peripheral band around the nucleoplasm and is bounded by the plasma membrane. The thickness of such a cytoplasmic band is irregular throughout the cell (Fig. 2b), sometimes having discontinuities in which the nucleoplasm is in direct contact with the plasma membrane. The main cytoplasmic elements are electron-lucent vesicles, mitochondria and myelin-like bodies (Fig. 2c-f). The cytoplasmic background mainly consists of granular material and anastomosing membranes (Fig. 2e). Numerous vesicles about 0.3 µm in size occur at the very periphery of the cytoplasmic band, often causing slight bumps in the sperm surface (Fig. 2c). As a result of this, the vesicle and plasma membranes are tightly apposed at the zone of contact of both (Fig. 2d). The peripheral clear vesicles contain a moderately electron-dense substance which either accumulates in a small core or forms a thin layer on the inner side of their membrane (Fig. 2d). Mitochondria occur in numbers of approximately 1-3 per section. They show randomly distributed cristae (Fig. 2 e, f).

FIG. 2. — Scanning (**A**) and transmission (**B-J**) electron micrographs of *Aristaeomorpha foliacea* spermatozoa. **A, B:** Sperm mass in the ampulla. **C:** Radial section of spermatozoon showing the peripheral cytoplasmic band and central nuclear region. **D-F:** Diverse details of peripheral cytoplasm to show the main cytoplasmic elements: peripheral electron-clear vesicles, mitochondria, dense myelin-like bodies and anastomosing membranes (asterisk). **G-I:** Myelin-like bodies appear to be released from the cytoplasm and occasionally may occur either out of the cell (**I**) or in the nucleoplasm (**G**). **J:** The nucleoplasm frequently shows nodules (asterisks) where the chromatin fibres become densely entangled. c; perinuclear cytoplasm; m, mitochondria; mb, myelin-like bodies; n, nuclear region; v, peripheral vesicles.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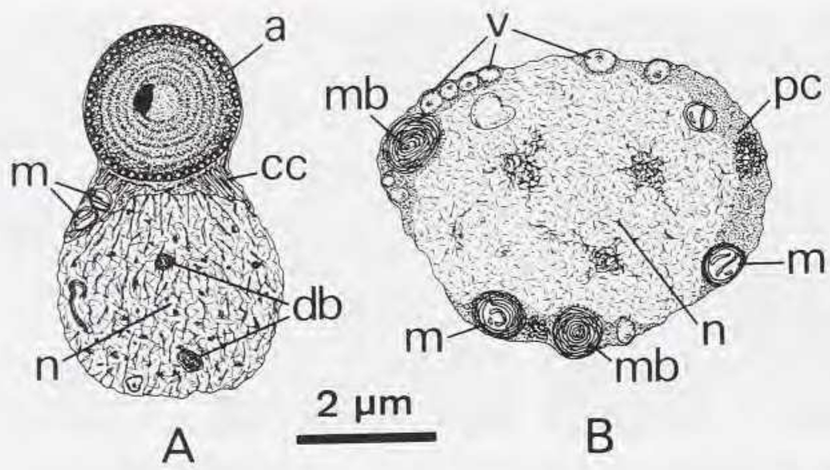

FIG. 3. — **A:** Spermatozoon of *Aristeus antennatus*. **B:** Spermatozoon of *Aristaeomorpha foliacea*. Drawn from transmission electron micrographs. a, acrosome; cc, cytoplasmic collar; db, dense bodies; m, mitochondria; mb, myelin-like bodies; n, nuclear region; pc, perinuclear cytoplasm; v, peripheral vesicles.

Myelin-like bodies apparently originate by coalescence of waste cytoplasmic membranes into concentric layers. Frequently, membrane layers become deposited around (Fig. 2e) or constitute dense bodies in close association with mitochondria (Fig. 2e, f). Isolated myelin-like bodies can be encountered not only in the cytoplasmic band, but also within the nucleoplasm (Fig. 2g). Some images suggest that at least some of them are extruded at the cell periphery (Fig. 2g-i).

As typical for all dendrobranchiates, the chromatin of *A. foliacea* sperm shows an uncondensed reticulate pattern and is not bounded by a nuclear envelope. It is characteristic that in this species nodules where chromatin fibres become more densely entangled are present (Fig. 2j).

DISCUSSION

The sperm morphologies of the Aristeidae *Aristeus antennatus* and *Aristaeomorpha foliacea* are markedly inconsistent with the dendrobranchiate unistellate sperm plan. While the unistellate spermatozoa of most dendrobranchiates consist of a main body housing the nucleus and an acrosomal complex formed by cap region and prolonging spike (see reviews by FELGENHAUER & ABELE [5], JAMIESON [9], KROL *et al.* [11]), the sperm of *A. antennatus* have a spike-less acrosome and those of *A. foliacea* lack any acrosomal structure at all.

Unlike the other studied dendrobranchiates, the spermatozoa of *Aristeus antennatus* lack a perinuclear cytoplasmic band, so that the nucleoplasm is bounded by only the plasma membrane in most of the nuclear profile. In gross morphology, these features liken the *A. antennatus* spermatozoon to that of reptant Pleocyemata, in particular Anomura [7, 8, 18, 25, 26] and Astacidea [2, 19, 24], in which the acrosome is prominent and lies fairly apart from the posterior nuclear region, with the cytoplasmic region located in between. Albeit these features are common to *A. antennatus* sperm, the spherical acrosome of the latter has no basal invagination as does the acrosomal vesicles in the above-noted reptants. In such a respect, this spermatozoon would be similar to that of the Palinuridae [13, 23]. Nevertheless, in spite of the several coincidences, there exist notable dissimilarities with regard to the general reptant sperm morphology, such as the absences of nuclear envelope and nuclear arms or the different substructure of the acrosome.

From the above comments, it is concluded that the spermatozoon of *Aristeus antennatus* simultaneously blends typically dendrobranchiate and typically reptantian characteristics, whereby its placement into one of the two traditionally established decapod sperm categories becomes difficult. Available ultrastructural descriptions of spermatids in this species [4] reveal a mechanism of acrosome formation resembling the one observed in many species of Pleocyemata [1, 6, 10, 12, 13, 15-18, 20]. However, it slightly differs from that described for the only two other Dendrobranchiata in which spermiogenesis has been ultrastructurally investigated, *Sicyonia ingentis* (see [21]) and *Parapeneus longirostris* (see [14]). Actually, the complex ultrastructural arrangement of the acrosomal vesicle contents in *A. antennatus* mature sperm is not comparable with that of other decapods. The absence of either a spike or any other significant structure at the place where the spike should supposedly lie, as well as the spherical (not capping) acosome with varied contents, are to be considered as clear autapomorphies within the Dendrobranchiata. Another assumed apomorphic character is the subacrosomal (instead of the plesiomorphic perinuclear) cytoplasm.

The most significant feature of the ellipsoid, appendage-less sperm of *Aristaeomorpha foliacea* is the amazing absence of any kind of acrosomal structure, which is unique in the Dendrobranchiata. Despite thorough examination of spermatozoa from both vasa deferentia from males and seminal receptacles from females, no trace of any structure that may be related to an acrosome was found. Hitherto, acrosome lack in Eumalacostraca was only known in Euphausiacea [9] and in Decapoda Stenopodidea [5]. As up to date *A. foliacea* is the only known case of dendrobranchiate sperm lacking the acrosome, one would be inclined to infer that this pattern has been reached by simplification from a peneoid-like (spiked) spermatozoon through evolutionary loss of the acrosome. Nevertheless, the findings of acrosome-less spermatozoa resembling the one of *A. foliacea* in Euphausiacea [9], Stenopodidea [5] and Sergestoidea [see MEDINA, this volume] suggest that the absence of the acrosome would be a primitive condition in Eucarida. Therefore, if the absence of the acrosome is plesiomorphic, the acrosome of *Aristeus antennatus* sperm represents a secondary acquisition, hence an apomorphy, within the Aristeidae. On the other hand, the spiked acrosome would be a synapomorphy of Penaeidae and Sicyonidae.

Well-known spermatozoal symplesiomorphic features of the Decapoda are the diffuse chromatin, partial or total disruption of the nuclear envelope and absence of flagellum. In addition, the present study confirms as clear plesiomorphies in Dendrobranchiata: a) non-membrane bound nuclear region, b) filamentous chromatin, c) perinuclear cytoplasm, d) absence of centrioles and radial arms. The reduced subacrosomal distribution of the cytoplasm in *Aristeus antennatus* should thus be considered as an autapomorphy. In conclusion, two distinct evolutionary trends appear to have occurred in Aristeidae, leading to sperm morphologies which are distant from the dendrobranchiate sperm plan exemplified by the assemblage Penaeidae-Sicyonidae. This suggests that, although ultrastructural studies on crustacean spermatozoa are generally useful for phylogenetic approaches, one must be cautious in certain instances, since notable variation may occur in close taxa [5].

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